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RATE OF MULTIPLICATION OF THE HESSIAN FLY.

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INTRODUCTORY AND HISTORICAL.

In the course of investigations of the Hessian fly (*Phytophaga destructor* Say) and its parasites, at the Cereal and Forage Insect Field Station of the Bureau of Entomology at Carlisle, Pa., it became necessary to have accurate data regarding the normal rate of multiplication of this insect. Such information was needed, in the first place, as a basis for estimating the efficiency of the various species of parasites. In the second place, the writer, having been greatly impressed by the rapidity with which an outbreak of serious proportions may develop in a short time from comparatively small sources, and being aware that such an increase is largely due to the reduction in effect of some of the important natural checks to the increase of the fly, suspected nevertheless that the potential rate of multiplication might be much greater than usually has been supposed.

The writer has been unable to find satisfactory data on this subject in the literature or among other recorded observations. In fact, it appears that little attention has ever been paid to the matter, especially

[1] Died June 23, 1920.

in recent times. In 1861 Wagner[2] by confining a female Hessian fly with wheat plants secured a total of 83 eggs. He evidently carried out other experiments, for he concludes that the number of eggs deposited by a female is more than 80 and less than 100. Koeppen[3] in 1889 stated that, according to Lindemann, a female may deposit up to 200 eggs, but believed these figures too high and gave Haberlandt's statement that the female deposits only from 40 to 50 eggs.

The most careful observations up to the present time seem to be those made by Enock.[4] He confined the female insects in cages with barley plants, securing in one case a maximum of 158 eggs. He also confined females singly in corked vials and secured in this way a maximum of 130 eggs. The number of eggs he secured by these methods ranged from 70 to 158, with an average for 10 cases of 113 eggs. He concludes that a single female lays from 100 to 150 eggs. Although Lugger[5] dissected a female which contained 238 eggs, the usual figures given since the date of the paper by Enock are based on Enock's conclusion. This conclusion, however, resulted from an insufficient number of experiments, and the methods used in obtaining the counts will not give accurate results. The adults of the Hessian fly are extremely sensitive to conditions of temperature and moisture. The females normally oviposit at comparatively low temperatures and when moisture in abundance is present. If these conditions are reversed or if conditions are unsatisfactory in some other respect, the females will die before depositing all their eggs. A new and thorough study of the subject therefore seemed imperative.

METHODS OF INVESTIGATION.

For the reasons stated, the method of confining female Hessian flies in vials and all other methods involving their confinement in cages kept in the laboratory were rejected. Cages kept outdoors at the usual times when adults are abroad were also dispensed with, because any cage modifies natural conditions, more or less, and because it is difficult to secure accurate counts where eggs are scattered over a number of plants.

The writer is convinced that under normal conditions each female deposits practically all of her eggs. It has been found that at the time of eclosion each female contains her normal allotment of eggs in a well-developed condition; in fact, it is possible to count all of the eggs by dissecting the pupa stage. It seemed simpler and more

[2] WAGNER, BALTHASAR. OBSERVATIONS ON THE NEW GALL-GNAT. Fulda, 1861. Translated in U. S. Entomological Commission, Third Report. Appendix II, B, 1883, p. [15].

[3] KOEPPEN, F. T. DIE SCHAEDLICHEN INSEKTEN RUSSLANDS. St. Petersburg, 1880. Translated in U. S. Entomological Commission, Third Report, Appendix IV, 1883, p. [41].

[4] ENOCK, F. THE LIFE-HISTORY OF THE HESSIAN FLY, CECIDOMYIA DESTRUCTOR, SAY. *In* Trans. Ent. Soc. London, p. 332, 1891.

[5] LUGGER, O. THE HESSIAN FLY. *In* Minn. Agr. Exp. Sta. Bul. 64, p. 552, 1899.

economical of time, therefore, to dissect the females and count the number of ova they contained, and this procedure has been followed out beginning with the fall brood of 1918.

Before the dissection of female flies and the counting of their ova had been carried very far, other difficulties appeared. These hinged chiefly on the question of what females should be counted. At first it seemed simple enough to count the number of ova contained in a given number of females and average up the results. This, however, proved to be insufficient because of the great variation in the results obtained from different lots of females. The females vary greatly in size, and, correspondingly, in the number of ova they contain; and the average number of ova per female varies in different fields.

In the study to determine some of the reasons for this condition of affairs, it became evident that the number of ova contained in a female is related to the number of puparia in a tiller. On the average, the greater the number of puparia in a tiller the smaller the number of eggs the resulting females can lay. Since the average number of puparia in infested tillers varies in different fields and in different years, the difficulty of making a fair average can be readily seen. There also appears to be a relation between the date when wheat is sown and the average number of eggs for females of the fall brood. Puparia obtained from late-sown wheat developed females with a reduced capacity for egg production. When work was begun on the spring brood in 1920 it was found that the average number of eggs varied markedly for the two principal generations. All of these conditions and undoubtedly others have to be dealt with in some manner in arriving at a fair estimate.

In view of these facts, separate counts have been made for the principal generations. In the case of the fall brood all of the puparia found in a number of plants taken from various fields were caged and every female which emerged was dissected. Most puparia were taken from fields known to be sown early and which, consequently, contained flies of all ages; or else they were taken from fields where the age of the plants was unknown. This avoided the giving of undue weight to fields sown late. In this manner many of the data accumulated have been eliminated from the general average for the fall brood.

In the case of the spring brood, all plants were obtained from a number of fields just before harvest. All their puparia were removed and caged. In two cages extremely long stubbles, which probably contained all the puparia of the original plants, were used. In this generation allowance must be made for an enormous mortality due to parasitism and weather. Usually it is not expected that more than from 3 to 10 per cent of the flies will remain alive at emergence time in the fall, and, of course, allowance must be made

for males which are sure to emerge. Taking all of these facts into consideration, success beyond expectations was achieved in the fall of 1919, in making counts for the spring brood of 1920.[6]

AVERAGE NUMBER OF OVA FOR THE PRINCIPAL BROODS.

In presenting the results of this investigation, it will be necessary to consider first the average number of ova which can be laid by females of the principal generations. The data for each of these generations will be tabulated separately. After this has been done, it will be necessary to take into consideration the proportion of the two sexes before a sufficient basis can be had for estimating the rate of reproduction of the Hessian fly.

FALL GENERATION.

In Table 1 are given the results of counting the number of ova contained in 107 females. These flies were obtained from six different fields, as indicated by their cage numbers. It will be noted that the average number of eggs per female varies considerably in different fields, even when the number of females counted is approximately the same. It is thus easy to see what a difficult matter it is to obtain a fair average number of eggs per female. The figures, however, are as fair as could be obtained for the year in question and in the time available.

TABLE 1.—*Average number of ova for females of the fall generation of the Hessian fly, Carlisle, Pa., 1919.*

Cage No.	Number of females counted.	Number of ova.	Minimum per female.	Maximum per female.	Range.	Average per female.
1620	28	8,014	74	383	309	286.0
1716	26	6,148	33	365	332	236.2
1753	36	13,422	189	464	275	372.8
1755	9	1,361	107	195	88	151.2
1779	6	1,099	134	302	168	183.2
1795	2	658	314	344	30	329.0
Totals	107	30,702	33	464	431	286.9

The actual number of ova per female varies from 33 to 464, with a range of variation of 431 and an average per female of 286.9. It may be added that the smallest female found since this work began belonged to this brood, but to none of the foregoing cage numbers. This female was dissected by Mr. Hill, who found that it contained only 11 ova. The largest female ever found belonged also to this brood. This female was in a different series and contained 474 ova.

[6] In this connection the writer wishes to state that two lots of females of the fall brood were dissected by Mr. C. C. Hill; Mr. P. R. Myers has determined the sex of a large proportion of the flies as they emerged, and both men have helped in collecting and caging the material. All of the work has been done in the laboratory at Carlisle, Pa., and most of the material has been collected near by.

SPRING GENERATION.

For the spring generation the ova have been counted for 160 females. The most surprising thing about the results obtained, as shown in Table 2, is the general average number of ova per female of 232.9. This is an average of 54 eggs per female less than was found in the case of the fall brood.

TABLE 2.—*Average number of ova for females of the spring generation of the Hessian fly; counts made at Carlisle, Pa., in the fall of 1919.*

Cage No.—	Number of females counted.	Total number of ova.	Minimum per female.	Maximum per female.	Range.	Average per female.
1841	57	14,591	79	386	307	256.0
1842	29	6,990	113	372	259	241.0
1869	4	780	34	297	263	195.0
1875	13	3,105	188	350	162	238.8
1876	5	836	71	255	184	167.2
1880	8	1,356	102	214	112	169.5
1881	6	1,048	100	227	127	174.7
1882	2	483	194	289	95	241.5
1883	26	5,965	116	370	254	229.4
1891	10	2,106	108	309	201	210.6
Totals	160	37,260	34	386	352	232.9

While this work has been carried through only one spring generation, it is nevertheless quite evident that this generation is constantly lower than the fall generation in its capacity for egg production. The actual minimum number of ova per female is 34, which is one more than for the fall brood. The maximum, 386, on the contrary, is much lower, and the range of variation is only 352.

SUMMER GENERATION.

While data for the flies developing in volunteer wheat are scant, the results obtained seem interesting enough to be included as Table 3. Only 15 cases are available. In spite of the low average number of eggs, this brood in all probability resembles rather closely the fall generation in the number of eggs it can lay. If this should prove true, it might be that the stage of growth of the plant has an important relation to the size of the flies developing in a plant, and consequently to the number of ova developing.

TABLE 3.—*Average number of ova for females of the generation of the Hessian fly developing in volunteer wheat; counts made at Carlisle, Pa., in the summer of 1919.*

Cage No.	Number of females counted.	Total number of ova.	Minimum per female.	Maximum per female.	Range.	Average per female.
1990	2	524	177	347	170	262.0
2090	13	3,027	54	448	394	232.8
Totals	15	3,551	54	448	394	236.7

SEX RATIO.

Before proceeding further with the discussion of the rate of multiplication, it is necessary to take up the question of the proportion existing between the two sexes. In order to acquire data on this subject, a beginning was made, more than two years ago, to record the sex of all Hessian flies that emerged in the cages. These cages contained only puparia separated from their surrounding plant tissue and reared in small vials. The puparia had been obtained in various localities in the northeastern portion of the United States. In this way the sex has been recorded of practically every fly that has emerged from a few thousand puparia each year. At the end of the first year it appeared that the percentage of females in the spring generation was remarkably high. It was not anticipated that this excess of females in the spring generation would prove to be constant, but Table 4 shows that for the second year the percentage of females dropped only slightly. Although the rearing of flies from the 1919 material has not been completed, a much larger number than usual have already been obtained, and the percentage of females for 1919 is almost the same as for the two preceding years.

TABLE 4.—*The sex ratio in the various Hessian fly generations, 1917, 1918, and 1919.*

Generation.	Year.	Number of males.	Number of females.	Total reared.	Per cent of females.
Spring	1917	168	276	444	62.2
	1918	146	235	381	61.7
	1919	623	1,031	1,654	62.3
Fall	1917	749	761	1,510	50.4
	1918	1,493	1,313	2,806	46.8
Volunteer wheat	1917	246	225	471	47.8
	1918	51	45	96	46.9

For the three years the average percentage of females is 62.1, and it seems quite safe to assume now that at least 60 per cent of the spring brood develop into females. In the case of the fall generation the sexes appear to be approximately equal in numbers, although figures for 1918 are rather low in females. In volunteer wheat there are a very small number of cases from 1918, but it appears in general that the sexes are about equal in the partial broods developed in the summer.

It is now evident enough that the spring brood is the one which shows the greatest variation from normal, both in the high percentage of females produced and in the reduced number of eggs these females can lay. Both may be related phenomena with a common explanation, but this explanation will have to be left to the imagination at the present time.

THE MEANING OF THESE FIGURES.

In order to demonstrate fully the meaning of the figures which have been submitted, two examples will be of considerable help.

Going on the assumption that under normal conditions practically every egg is laid, let it be assumed that none of the fly stages are destroyed by enemies. For the sake of round numbers let 285 be taken as the average number of eggs laid by the fall generation and 230 as the average by the spring generation. It may also be taken for granted that one male will fertilize several females, since Enock [7] proved by careful methods that one male successfully fertilized as many as six females. This will take care of the preponderance of females in the spring brood.

Starting now with a single female of the spring brood emerging in the fall, it is found that she can lay 230 eggs. One-half of these eggs in the spring will produce females, each of which may lay 285 eggs. This will give 32,775 as the product of one female working through two generations in one wheat crop, with no allowance made for multiplication in volunteer wheat. The flies which develop in volunteer wheat in the East are usually comparatively small in number and are heavily parasitized. If it be assumed that all these flies remain alive in the stubbles until the next fall, there will be a total of 60 per cent of the flies emerging as females, or 19,665. If these all lay 230 eggs, there will be the enormous total of 4,522,950 flies developing in the fall wheat of the second year. The resulting females would number 2,261,475 and would give rise in the second spring to 644,520,375 fly stages. This result has been obtained in two crop years, not allowing for any multiplication in volunteer wheat.

The question may be looked at from another point of view. Probably infestation of stubbles is never as low as one puparium per acre, although the foregoing computation began with one fly. In one field studied quite carefully during the summer and fall of 1919 the stubbles were found to be infested at the rate of 4,900,000 per acre. A careful examination of the puparia in these stubbles just before the emergence season showed that only 4.4 per cent contained living fly larvae, parasites having destroyed practically all of the remainder. This 4.4 per cent amounts to 215,600 flies per acre. If 60 per cent of these were females there would be 129,360 females per acre ovipositing in the next crop of wheat and producing in it the next fall 29,752,800 ova. With similar calculations from a few other fields as a basis, a big outbreak in wheat sown in the fall of 1919 was looked for. As a matter of fact, however, it was found after the emergence season was over that many of the expected flies had failed to emerge from the stubbles. A careful count made in the field mentioned above showed that only about one-third of the healthy fly larvæ had transformed. This amounted to about 1.4 per cent of the total number of flies.

[7] Op. cit.

Correcting the figures to correspond with what actually happened in the field and calculating in the same way as before, it is found that this extremely small percentage of flies transforming in this stubble field in the fall would amount to 68,600 flies per acre, with 60 per cent or 41,160 females. These females would lay enough eggs to develop into 9,466,800 flies per acre in young wheat sown in the fall of 1919. This is a much smaller number than had been anticipated, but it will be readily seen that even this is an enormous infestation. If the farmer sows about the same acreage from year to year and no flies are lost by migration, then the flies from an acre of stubbles would proceed to an acre of new wheat. It is calculated that 1,000,000 plants per acre is a good stand, and in that case this farmer would have over nine flies developing on every wheat plant. It will be readily seen from this that his chances of securing a wheat crop under the conditions named are practically zero. It is also evident that anything which helps to cut down this rate of reproduction is of enormous benefit. The principal checks to the multiplication of the Hessian fly are its parasitic enemies and unfavorable weather conditions, and if it were not for them it probably would be impossible inside of two years to grow wheat at all. This illustration, it is hoped, will also help to explain how an outbreak may seem to develop suddenly from a very low infestation of stubbles.

CONCLUSIONS.

The principal points made in this bulletin may be summarized as follows:

1. The rate of multiplication of the Hessian fly is much higher than has been realized.

2. The rate of multiplication is quite different in the two principal broods of the Hessian fly, the spring brood laying on an average only about 230 eggs per female, whereas the fall brood lays about 285 eggs per female.

3. The capacity for reproduction also varies with a number of other factors, such as date of sowing, number of puparia per tiller, etc.

4. Because of these various influences, the actual rate of multiplication will be found to vary from year to year and even from field to field, and in years of light infestation the figures will prove too low.

5. The proportion of males to females varies in the two principal generations. In the spring generation about 60 per cent of the flies are females; in the fall generation the sexes are approximately equal in number.

6. By applying these figures, however unsatisfactory the basis may be, it is believed that entomologists will be better able to appreciate how a Hessian fly outbreak may develop very suddenly, and to predict in a more accurate manner the approach of a dangerous outbreak.

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